

Suspension Feeding Adaptations to Extreme Flow Environments in a Marine Bryozoan

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Abstract. We describe the effects of extreme flow on the growth and morphology of a bryozoan, *Membranipora membranacea*, encrusting laminarian fronds in the Rapids of Lough Hyne (=Ine), County Cork, Ireland. An ultrasonic current meter was used to characterize ambient flow regimes at the level of the algal canopy over a complete tidal cycle at three sites within the Rapids. Colonies collected from sites exposed to different flows showed a trend towards miniaturization with increased flow; the zooids were less elongate, the lophophores were smaller in diameter and had fewer tentacles, and the distances between excurrent jets were shorter. These morphological changes probably place feeding surfaces into slower flow regimes of the boundary layer. Similar growth rates of colonies at sites differing in flow provide evidence that this miniaturization is adaptive and that bryozoans are capable of adopting appropriate morphological responses to varying environmental regimes. Such plasticity should be considered when assessing feeding from different flow regimes because particular colonies may be adapted to a limited and specific range of flow conditions.

Introduction

Many aquatic organisms, ranging from microbes to whales, have the ability to collect food particles from the water column. Whereas mobile suspension feeders collect particles by actively swimming through the water, sessile suspension feeders rely on the movement of water to carry food resources to their feeding surfaces. In both cases, the potential food available is determined by the flux of particles past feeding surfaces, which is a function of particle

concentration and the rate at which these particles are encountered by the feeding surfaces. All else being equal, increased flow will increase the flux of food to sessile suspension feeders. It will also result in increased turbulent mixing of the surrounding water, which reduces depletion of food particles near feeding surfaces (Wildish and Kristmanson, 1979; Patterson, 1984; Fréchette and Bourget, 1985; Fréchette *et al.*, 1989).

Despite these benefits of flow, too much flow will eventually be detrimental, as indicated by a decline in feeding rates at higher flows in a variety of suspension feeders (*e.g.*, Okamura, 1984, 1985, 1992; McFadden, 1986; Best, 1988; Leonard *et al.*, 1988; Sponaugle and LaBarbera, 1991; Eckman and Duggins, 1993; Anthony, 1997). These declines are explained by deformation of filtering structures that reduces surface areas for particle capture, drag effects that reduce efficiency of handling or processing particles, adverse pressure gradients that inhibit effective processing of water in feeding, or a combination of these factors (Eckman and Duggins, 1993). These considerations suggest that sessile suspension feeders may avoid extreme flow conditions by (1) not feeding during inappropriate flow conditions, (2) colonizing appropriate flow habitats, or (3) employing flow-dependent morphological responses that allow them to exploit particular flow microhabitats.

A number of studies have examined the effects of flow on growth and feeding of active suspension feeders including bivalves (*e.g.*, Kirby-Smith, 1972; Eckman *et al.*, 1989; Grizzle *et al.*, 1992; Lenihan *et al.*, 1996; Judge and Craig, 1997), barnacles (Eckman and Duggins, 1993), bryozoans (Okamura, 1984, 1985, 1990; Eckman and Duggins, 1993; Grünbaum, 1995), and serpulids (Eckman and Duggins, 1993), although only one study has demonstrated that the effect of flow on feeding translates into flow effects on growth (Okamura, 1992). Except in sponges, whose morphologies vary with exposure to flow (Wilkinson and Vace-

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let, 1979; Palumbi, 1984), the morphological responses to flow of active suspension feeders have received little attention.

Studies of cnidarians indicate that morphological changes can enable passive suspension feeders to exploit a range of flow environments. For instance, individuals of the sea anemone *Anthopleura xanthogrammica* are found in flow conditions ranging from exposed intertidal surge channels to protected crevices. Koehl (1977) showed that variation in the shapes of anemones resulted in exposure to similar flow forces in these two types of habitats. Thus taller anemones in protected habitats encountered flows as fast as those experienced by squat anemones in surge channels because squat anemones hide in the reduced flow regimes of the benthic boundary layer, whereas tall anemones extend into the freestream flow regime beyond that layer. Similarly, Anthony (1997) reported large individuals of the anemone *Metridium senile* to occur in regions of low currents and small individuals in narrow channels with greatly increased current speeds. He found that feeding rates were dependent on anemone size and hence were related to habitat. Large anemones thus experienced an inhibition in feeding at increased flows, but the feeding rate of small anemones was unaffected. These studies indicate that plasticity in body size and shape may allow anemones to avoid the feeding inhibition that occurs in faster flows by ensuring that feeding surfaces experience similar flow microhabitats even though the anemones may be found in strikingly different flow macrohabitats.

Here we address how flow affects the growth rates and the associated morphological responses of an active suspension feeder by studying colonies of the bryozoan *Membranipora membranacea* along a gradient of extremely rapid flow in a tidal channel in southwest Ireland.

Materials and Methods

The study system

The Rapids of Lough Hyne (=Ine) (County Cork, Ireland) present an ideal site for studying growth and morphological variation along an environmental gradient of flow. In the Rapids, tidal water is forced to flow through a relatively narrow channel that connects an inland marine lough with the sea (Fig. 1). Flows reach highest speeds in the narrowest and shallowest region of the Rapids known as the "Sill," which is about 1 m deep at low water and is bordered on the west by a seawall. The site is subject to simple flows with no confounding wave action; near-maximal flows are maintained during much of the inflow and outflow periods, and the period of slack water is of very short duration (Bassindale *et al.*, 1948; data reported here). Organisms living in the Rapids are thus subjected to highly predictable flow regimes, the characteristics of which are determined principally by their location within the Rapids channel. However,

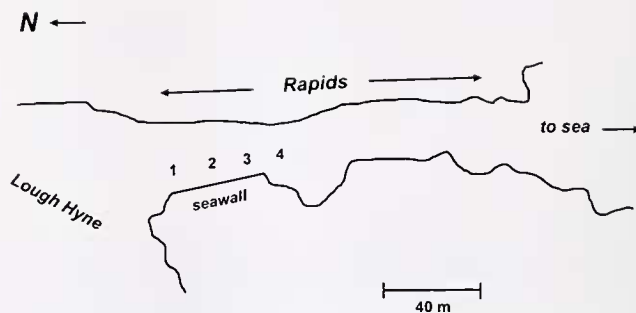


Figure 1. Schematic of the Rapids of Lough Hyne showing sites where flow measurements and growth studies were conducted (Sites 1–3) and from which colonies were collected for morphometric studies (Sites 1–4).

other than flow, environmental conditions are similar in different stretches of the Rapids because a large tidal volume is forced through the relative short and narrow region of the Rapids. Thus organisms within the Rapids will be subject to similar temperatures, salinities, food particle concentrations, etc.

Membranipora is an epifaunal bryozoan that specializes in encrusting the fronds of macroalgae, forming sheetlike colonies that grow rapidly (Seed, 1976) and can attain large sizes. *M. membranacea* is common on fronds of the laminarians *Laminaria digitata* and *Saccorhiza polyschides*, both of which grow in the Rapids area. Because these macroalgal fronds are highly flexible, colonies of *M. membranacea* will experience unidirectional flows as the fronds flex and become extended by incoming and outgoing tidal currents.

Flow measurements

We characterized the ambient flow regime at the canopy level of algal fronds at three sites along the Rapids by using an ultrasonic current meter (Minilab Model SD-12) that measured the velocity of flow in three dimensions with a resolution of 1 mm s^{-1} . Because of the strength of flow through the Rapids it was necessary to securely deploy the flow probe to ensure it was not displaced downstream or its orientation disturbed. We did this by attaching the probe to an aluminum pole fastened to the end of a ladder that extended outwards over the Rapids from a solid seawall. The aluminum pole and attached probe were lowered from the end of the ladder directly into the Rapids so that the probe was measuring flows at the level of the algal canopy. The ladder itself was weighed down with boulders, and we maintained the probe in a vertical position with a rope that was attached to the aluminum pole and held taut from an upstream position during flow measurements. This set-up was sufficient to ensure that the flow probe maintained a constant position in the face of strong tidal flows. The probe itself was placed in a cylindrical wire cage (diameter = 10 cm, height = 17 cm; mesh thickness = 0.2 cm; gap size =

1.7 cm) to protect it from water-borne objects. The caging may have contributed to the turbulence levels measured in the study, but such effects are greatest in low-energy environments (Nowell and Jumars, 1984) that are not characteristic of the Lough Hyne Rapids.

Measurement sites were chosen to represent a gradient of flow through the Rapids area in which *M. membranacea* colonies were growing on laminarian fronds (see Fig. 1). The exact location of measurements was determined by the availability of reasonably flat stretches of the seawall where a stable probe-and-ladder apparatus could be set up. Flows at each of the three sites were measured about 1 m from the wall, at the level of the algal canopy. Data collected represent instantaneous flow readings taken every second over a series of 5-min periods for each site over a complete tidal cycle. After each 5-min period, the probe and its ladder support were moved to the next site and reassembled to monitor for a further 5-min period. It should be noted that this sampling scheme may underestimate turbulence by overlooking high-frequency turbulent fluctuations over very short time scales. However, some of these fluctuations should be reflected in overall turbulence estimates because they contribute to the level of variation in flow that is sampled by the 300 or so data points accumulated over a 5-min period.

Our sampling regime provided an overall measure of flow at each site during both the inflow and the following outflow periods of a tidal cycle. We began monitoring flows at the end of the short slack-water phase when the laminarian fronds were observed to flop over with the incoming tide. The measurements were taken on 20 August 1995 during a period of neap tides and thus represent minimal ranges of tidal flow at the three sites.

Data on flow in the x (along the length of the Rapids), y (across the Rapids), and z (vertical) dimensions were used to determine the overall mean velocities and turbulent kinetic energy densities for each 5-min period. Overall mean velocities for each sampling period were calculated as the mean of individual determinations of $(u^2 + v^2 + w^2)^{1/2}$ sampled once per second over the 5-min period (where u , v , and w represent the flow velocities in the x , y and z directions). Turbulent kinetic energy density (joules per cubic meter; Clifford and French, 1993) summarizes the turbulent fluctuations in all three dimensions and was calculated by the equation

$$E = \frac{1}{2}\rho(\sigma_u^2 + \sigma_v^2 + \sigma_w^2)$$

using $\rho = 1.025 \text{ kg} \cdot \text{m}^{-3}$ (the density of seawater) and σ_u^2 , σ_v^2 and σ_w^2 the variances of the three components of flow over the 5-min periods of sampling in the x , y , and z directions.

Bryozoan responses to flow

We monitored growth rates of relatively small colonies of *M. membranacea* growing on fronds in the three sites in which flows were assessed. To ensure independence, we mapped and photographed only one colony per frond segment to monitor its growth. The frond segments containing the mapped colonies were marked by attaching cable ties to the mapped colonies. We attached a small piece of orange surveyor's tape to the cable tie, which helped us to relocate colonies. We chose colonies that were relatively isolated from other colonies on the frond segment and therefore would be unobstructed in growth. We mapped and photographed 8 colonies in Sites 1 and 2, and 13 colonies in Site 3. Because we were restricted to working in the Rapids during the short period of slow flow around the time of slack water, we required two consecutive days (17 and 18 August 1995) to set up the growth experiments. All colonies were allowed to grow for 10 days, and were then collected and rephotographed. The seawater temperature measured mid-way through the growth experiments was 19°C.

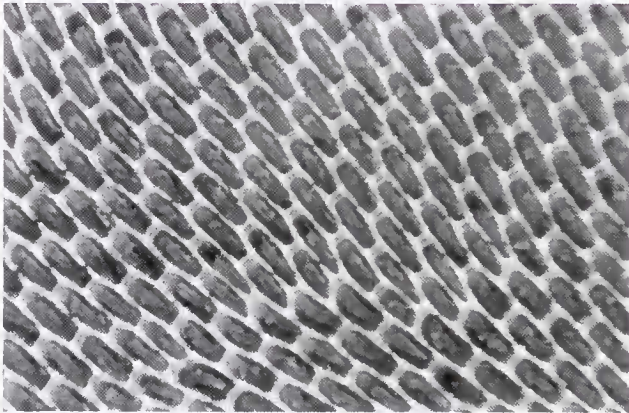
To assess morphological responses to flow, colonies were collected from within 1 m of the three sites at which flow was monitored. We also collected colonies from a fourth site at which flows were not measured because we could not securely deploy the probe in such rapid flow conditions. In the laboratory, a dissection microscope was used for morphometric measurements, which were accurate to the nearest 20 μm . For each colony we measured lengths, maximum widths (Fig. 2), lophophore diameters, and number of tentacles per lophophore of seven haphazardly chosen zooids. We avoided measuring zooids that are produced at early stages of colony development and had not yet achieved normal size, and the smaller zooids that develop initially in lineal series of zooids that are produced through bifurcation from a parental lineal series. We determined interchimney distances as the distance between the centers of neighboring chimneys (Fig. 3). Chimneys represent regions where ex-currents are jetted away from colony surfaces. We collected a fresh set of colonies from each site for these measurements; this ensured that the colonies were behaving normally and that the extended arrays of lophophores made the chimneys clearly visible. We attempted to measure nine interchimney distances per colony, although in a small number of cases fewer than nine were available for measurement.

We determined the relative densities of colonies in the three sites by assessing the percent cover of *M. membranacea* on three *Laminaria* and three *Saccorhiza* plants from each of the three sites. We randomly selected three fronds per plant and measured the percent cover of *M. membranacea* along a line transect running the lengths of the fronds.

We ensured that the data collected conformed to the assumptions of all statistical analyses used. If assumptions

of variance homogeneity in ANOVA could not be met through transformation of the data, we employed the non-parametric Kruskal-Wallis test. Morphometric analyses used mean values per colony as individual data points and are therefore reported as overall mean values. This approach allowed us to test specifically the overall differences in colonies from different sites, but it overlooks additional information on intra-colony levels of variation within and between sites.

A



B

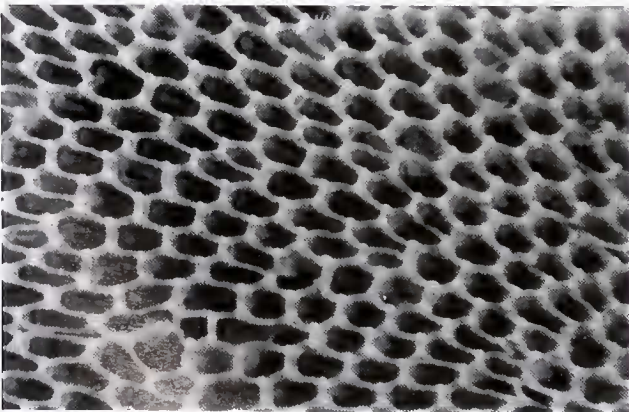


Figure 2. *Membranipora membranacea* colonies collected from slower and faster flow sites showing flow-associated variation in zooid shapes. (A) Zooids produced in colonies growing in slower flows assume elongate, nearly rectangular shapes. Note that zooid lengths were measured as the distance from the midline of distal edges of the end walls of contiguous zooids in lineal series, and zooid widths were measured as the maximum width observed between lateral zooidal walls (see Materials and Methods for discussion of choosing zooids for measurement). (B) Zooids produced in colonies growing in fast flows assume more hexagonal shapes and often possess wavering walls. Magnification = $\times 10$.

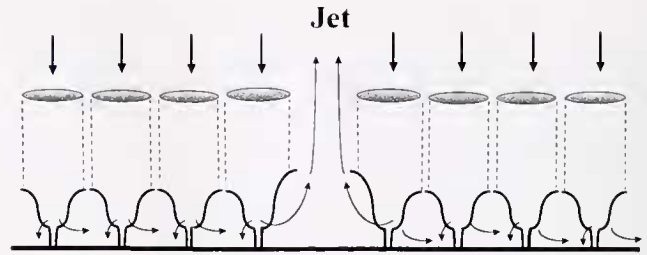


Figure 3. Schematic depiction of ciliary-driven movement of water (shown by arrows) over colony of *Membranipora membranacea*. Ciliary feeding currents produce feeding zones through which water is drawn into the lophophore. Water exits the bases of lophophores between the tentacles. Because lophophores are closely spaced, this excurrent flow is directed below the array of extended lophophores until it finds a gap, or chimney, where lophophores are not extended; it then escapes through this gap as a jet from colony surfaces. The relatively high velocity of the excurrent jet carries excursions to some height above the colony surface, which minimizes refiltration since jets are then carried away by boundary layer flow (Lidgard, 1981).

Results

Flow measurements

Flows differed at the three sites as expected, with Site 1 consistently experiencing the lowest flow speeds and Site 3 the highest (Fig. 4). The period of inflow (into Lough Hyne) was much shorter, and thus higher flows were sustained, than during the longer period of slower outflow. The upper plot of Figure 4 shows the overall mean velocities in the x , y , and z directions. In nearly all cases apart from several instances around the time of slack water, the major contributor to flow was in the x (downstream) direction due to the incoming and outgoing flows, as can be seen by the ranges of flows in each direction for each site during the inflow and outflow periods (Table 1). Turbulent kinetic energy density was consistently highest in Site 3 and lowest in Site 1 (see Fig. 4, lower panel), as might be expected from the flow velocities at the three sites, and was greater during inflow.

Bryozoan responses to flow

M. membranacea showed morphological variation for several traits along the flow gradient. Mean zooid lengths decreased from Sites 1 to 4, in association with the increase in mean (and maximum) flow velocities at these sites, although this trend was not quite significant (Kruskal-Wallis test: $H_{\text{adj}} = 7.491$, $df = 3$, $0.05 < P < 0.10$; Fig. 5a). There was no change in mean zooid widths among the four sites (Kruskal-Wallis test: $H_{\text{adj}} = 0.184$, $df = 3$, $P \geq 0.05$; Fig. 5b). Mean zooid elongation (zooid length/zooid width) significantly decreased with increased flow ($F_{3,30} = 4.106$, $P = 0.015$; Fig. 6a), but mean zooid areas (zooid length \times zooid width) did not differ among the four sites ($F_{3,30} = 1.411$, $P = 0.259$; Fig. 6b). These results indicate that zooids become less elongate largely through a decrease in

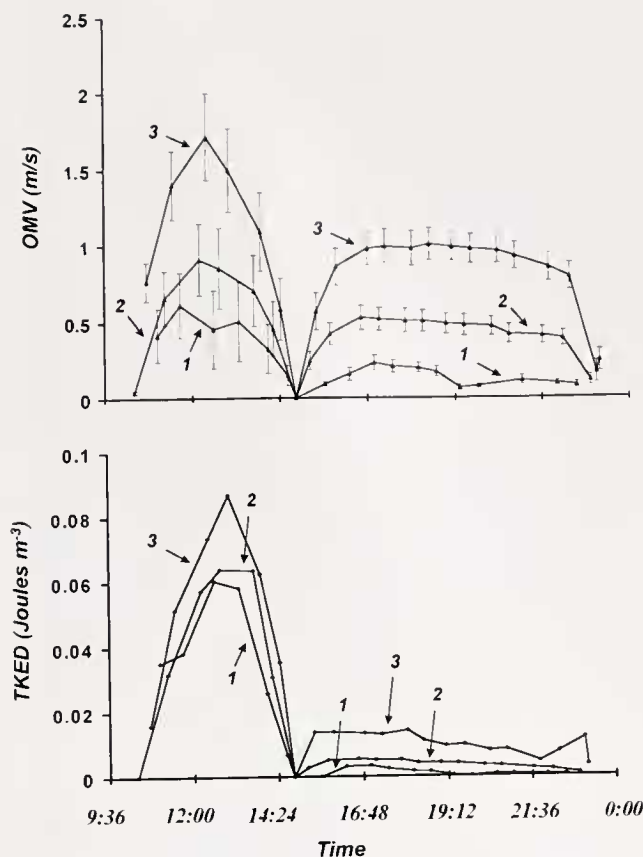


Figure 4. Two characterizations of ambient flow regimes at the algal canopy level for Sites 1–3. Sites are denoted by numbers, with arrows pointing to relevant data. Overall mean velocities (OMV) are plotted in the top graph and were calculated from flow measurements in the x , y , and z directions over 5-min intervals during inflow (from 1024–1450) and outflow (from 1513–2311) at Sites 1–3 (see Fig. 1). Bars represent one standard deviation. Values of turbulent kinetic energy density (TKED) are shown in the lower graph. See Materials and Methods section for details on flow measurements and characterization of the flow regimes.

length. There must also, however, be some slight increase in width—even though zooid width on its own did not vary significantly among sites (but see trend towards increasing width with increased flows; Fig. 5b)—since less elongate zooids in sites exposed to faster flows have areas similar to those of zooids in slower flow sites. Although we made no explicit attempt to compare zooid shapes, other than assessing zooid elongation, it was apparent that zooids in colonies exposed to the extremely rapid flows at Site 4 were irregular in outline. They were more hexagonal, often with wavering walls, than the normal elongate, fairly rectangular zooid with straight walls (see Fig. 2). This suggests that calculations based on data for maximum length and width may overestimate the zooid areas of colonies under conditions of very rapid flows. Such irregularly shaped zooids may be a character indicative of exposure to flow in *M. membranacea*.

Table 1

Ranges of mean velocities measured in the x , y , and z directions denoted as u , v , and w measured at Sites 1–3 during inflow and outflow tidal periods

Tidal Period	Site	Mean u ($m\ s^{-1}$)	Mean v ($m\ s^{-1}$)	Mean w ($m\ s^{-1}$)
Inflow	1	0.082–0.564	0.023–0.126	0.002–0.117
	2	0.411–0.866	(–0.026)–0.133	0.028–0.191
	3	0.548–1.652	0.022–0.186	0.199–0.436
Outflow	1	(–0.056)–0.133	0.013–0.178	(–0.0004)–0.052
	2	0.089–0.485	0.053–0.181	0.018–0.082
	3	(–0.230)–0.954	0.057–0.351	0.024–0.245

Data represent minimum and maximum values obtained over all 5-minute sampling periods conducted at each site during inflow and outflow.

The mean diameter of lophophores decreased significantly with increased flow (Kruskal-Wallis test: $H_{adj} = 13.657$, $df = 3$, $P < 0.005$; Fig. 7a). Coupled with the decrease in lophophore diameter was a decrease in the number of tentacles per lophophore ($G = 48.388$, $df = 6$, $P < 0.001$) (Fig. 8). Frequency analysis on data for number

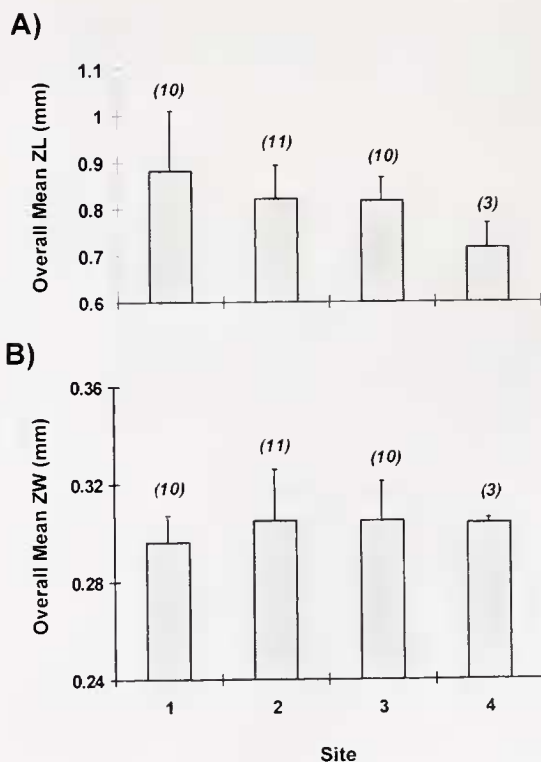


Figure 5. (A) Overall mean zooid lengths (ZL) per colony from colonies collected from Sites 1–4. (B) Overall mean zooid widths (ZW) per colony from colonies collected from Sites 1–4. Bars represent one standard deviation; n values in parentheses.

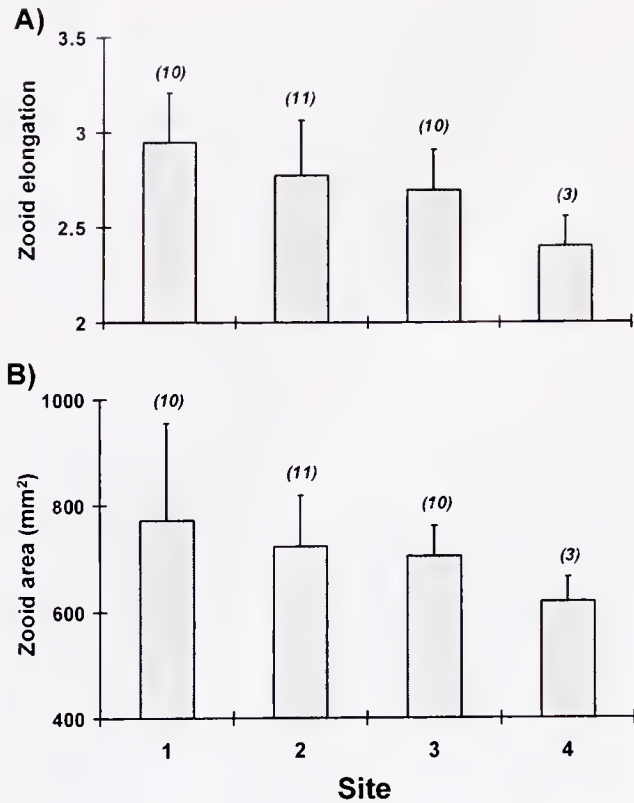


Figure 6. (A) Overall mean zooid elongation (zooid length/zooid width) per colony from colonies collected from Sites 1–4. (B) Overall mean zooid area (zooid length \times zooid width) per colony from colonies collected from Sites 1–4. Bars represent one standard deviation; n values in parentheses.

of tentacles per lophophore entailed pooling frequencies in the highest and lowest categories to avoid low expected values. Such pooling ensured that no more than 20% (in our case 8.33%) of expected values were less than 5 (in our case one expected value was 3.5) and therefore that the sampling distribution provided a good approximation of the χ^2 distribution (Cochran, 1954, cited in Siegel and Castellan, 1988). Smaller lophophores with fewer tentacles should also be shorter, although we made no direct measurements of lophophore height. This expectation is supported by the positive relationship between tentacle number and lophophore height in Best and Thorpe's study (1986) of a variety of British bryozoan species, including *Membranipora*, as well as Ryland's overall finding (1975) that all lophophore parameters are related to lophophore size and therefore are intercorrelated. We also found significant decreases in mean interchimney distances along the flow gradient ($F_{3,29} = 39.442$, $P < 0.001$; analysis on log-transformed data to ensure homogeneity of variances; see Fig. 7b). Thus, as ambient flows increase, colonies produce less elongate zooids with smaller lophophores, and excurrent flows travel shorter distances below these more closely

spaced and smaller lophophores before they are ejected as jets from colony surfaces.

For monitoring growth rates, we were able to relocate 6 of the 8 colonies photographed in Site 1, and 7 of the 8 colonies photographed in Site 2, but we failed to find any of the 13 colonies photographed in Site 3. We noted that the holes punched for attaching cable ties to algal fronds were often beginning to split along the length of the fronds, presumably due to drag forces, causing the cable ties to cut through and split apart the fronds. Indeed, in several instances we re-attached the cable ties to different locations on fronds when we noticed these splits developing. Thus it is likely that the drag forces in Site 3 were great enough to result in the loss of all cable ties and surveyor's tape used to mark the mapped and photographed colonies.

ANOVA indicated no significant differences in the initial sizes of colonies retrieved for growth analysis (Site 1: mean initial colony size = 317.5 mm², SD = 186.1, $n = 6$; Site 2: mean initial colony size = 368.4 mm², SD = 240.7, $n = 7$; $F_{1,11} = 0.1802$, $P = 0.6794$). Analysis of the growth increments of these colonies revealed no significant differences in the difference between mean final and initial col-

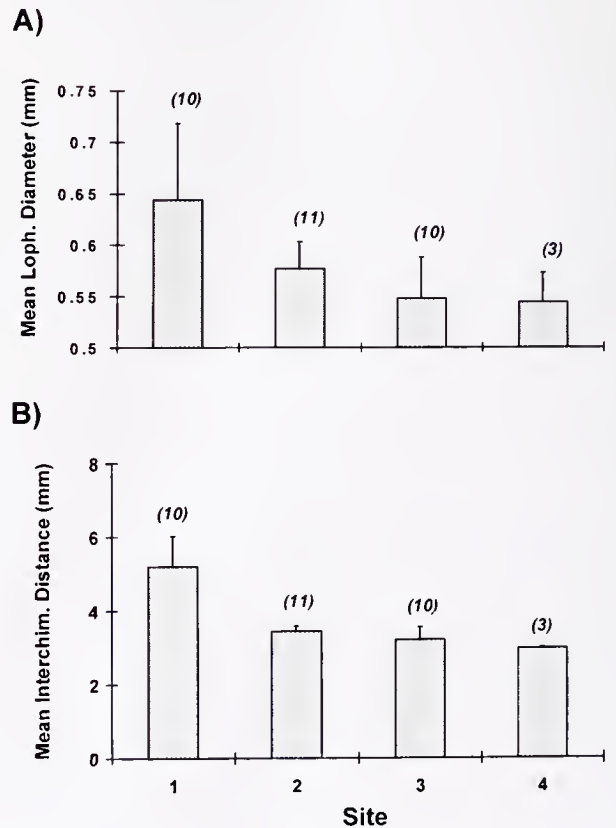


Figure 7. (A) Overall mean lophophore (Loph.) diameter per colony from colonies collected from Sites 1–4. (B) Overall mean interchimney (Interchim.) distances per colony from colonies collected from Sites 1–4. Bars represent one standard deviation; n values in parentheses.

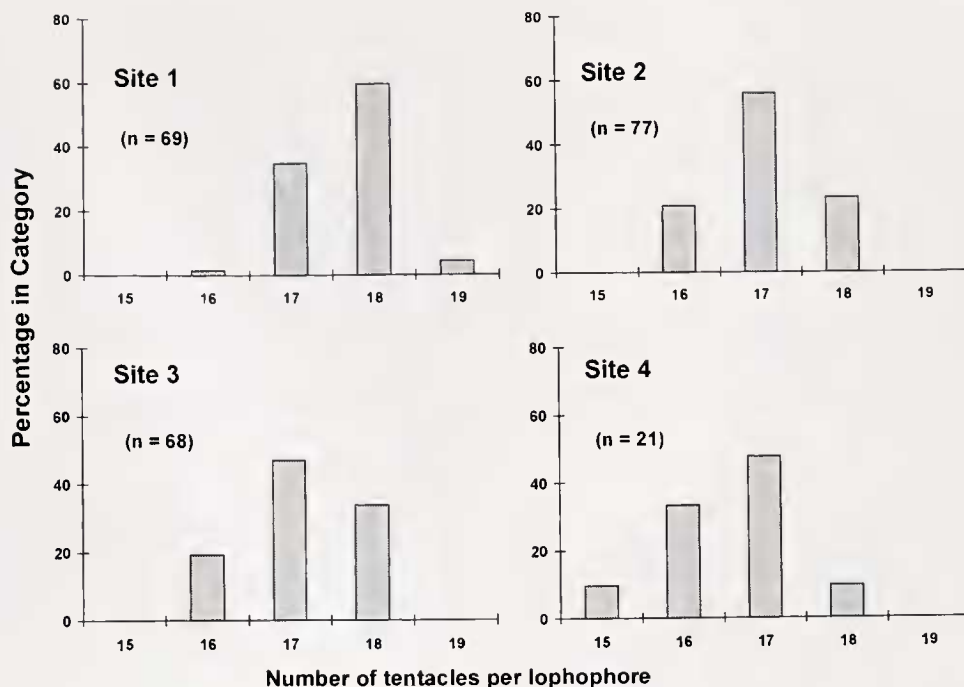


Figure 8. Percentages of lophophores with different numbers of tentacles in colonies collected from Sites 1-4.

ony sizes over the period of study ($F_{1,11} = 0.385$, $P = 0.548$; Fig. 9). Thus, although colonies showed a progressive miniaturization by producing smaller, more closely spaced lophophores with increased flow, there was no apparent effect of flow on growth rates at the two sites in which we were able to assess growth. It is unfortunate that our inability to relocate colonies in Site 3 meant we could not determine the extent to which flow continues to have no effect on growth; nevertheless, it is notable that decreases in zooid length and elongation, lophophore diameter, and

number of tentacles per lophophore continue along the entire flow gradient of the four sites. Since we did not retrieve any colonies from Site 3 for growth assessment and did not attempt growth studies at Site 4, it is not clear whether the irregularly shaped zooids are associated with poor growth rates in more extreme flows.

Concurrent with the miniaturization of colonies with increased flow was a decrease in percent cover (Fig. 10). ANOVA on arcsine-transformed data showed highly significant differences in cover between Sites 1 and 2 ($F_{1,37} = 34.548$, $P \ll 0.001$). We excluded Site 3 from the analysis as nearly all fronds had zero percent cover and we could find no transformation to meet the requirement of homogeneity of variance in ANOVA.

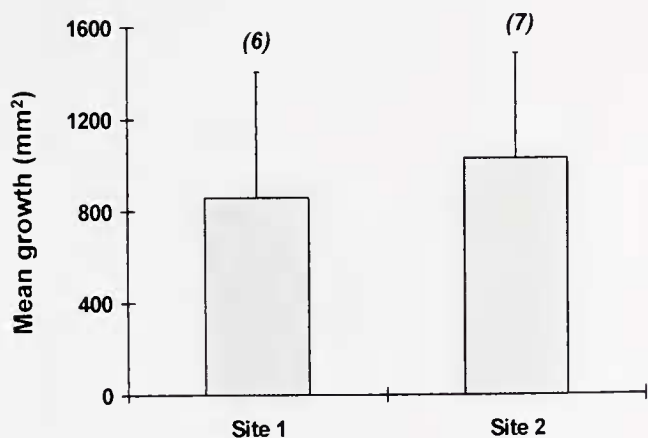


Figure 9. Mean growth increments of colonies over 10 days in Sites 1 and 2. Growth measured as final colony size minus initial colony size. Bars represent standard deviation; n values in parentheses.

Discussion

Adaptive miniaturization in response to ambient flow

Our study indicates that encrusting bryozoans respond to increased flow regimes by morphological changes that result in the miniaturization of sheetlike colonies. This response parallels that of anemones in which individuals become smaller or squatter in more exposed conditions. Such flow-modulated alterations in size and shape are probably beneficial because they should place feeding surfaces into the slower flow regimes of the boundary layer, thus allowing individuals to avoid excessive flows that are detrimental to feeding. Equivalent growth rates for *M. mem-*

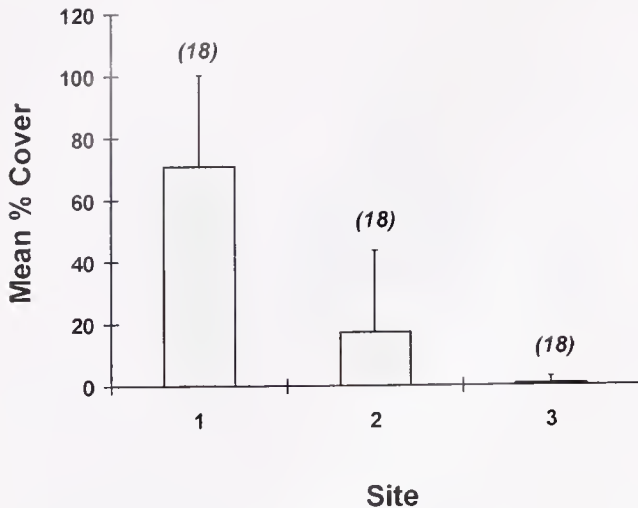


Figure 10. Mean percentage cover of laminarian fronds by *Membranopora membranacea* colonies in Sites 1–3. Bars represent one standard deviation; *n* values in parentheses.

membranacea colonies growing in Sites 1 and 2 suggest that these morphological changes are adaptive, in that they are expressed in colonies that achieve similar growth rates under different flow conditions, presumably because of similar rates of feeding. At some point, boundary layers will become so thin that further miniaturization is not feasible; however, the continuous decline in size shown by *M. membranacea* colonies over the four sites studied suggests that this critical point had not been reached.

Previous field investigations have obtained evidence that increased turbulence can have beneficial effects on growth (Wildish and Kristmanson, 1979; Patterson, 1984; Fréchette and Bourget, 1985; Fréchette *et al.*, 1989). However, while increased levels of turbulent kinetic energy density characterized the ambient flow regimes measured at the level of the algal canopy at Site 2, these were not reflected in increased growth rates of *M. membranacea* colonies. It may be that the bryozoans themselves do not experience the higher turbulence because the flexibility of algal fronds in response to three-dimensional flows, and the thickness of the boundary layer, reduces the relative movements of water over frond surfaces. Although Koehl and Alberte (1988) found that increased blade flapping in *Nereocystis luetkeana*, the giant bull kelp, stirs water near the blade surface, this effect was greatest at slow ambient flows and is unlikely to apply to the extreme flow conditions experienced by laminarian fronds in Lough Hyne. Alternatively, turbulence may have had no effect on growth in our study if food levels were not limiting.

It is notable that the percent cover of *M. membranacea* colonies decreased dramatically along the flow gradient: values near 100% on some fronds in Site 1 declined to 0% on most fronds by Site 3. Beyond Site 4, where flow

velocities were very great (and not measured), no colonies were evident. These patterns could reflect pre-settlement, settlement, or post-settlement events. The lack of colony development in sites exposed to extremely fast flows may be due to detrimental effects of flow on feeding that can no longer be overcome by increased miniaturization. It is also conceivable that larvae settle at much lower rates with increased exposure to flow, either because they actively choose not to settle or because drag forces prevent most of them from adhering to frond substrata. Yet another explanation—that the higher cover in Site 1 results from differential settlement patterns controlled by proximity to a source population of larvae within Lough Hyne—is unlikely because the larvae of *M. membranacea* are long-lived planktotrophs.

Our finding that growth rates were equivalent at Sites 1 and 2 contrasts with Eckman and Duggins' study (1993) in which the growth of very young colonies of *M. membranacea* was reduced at increased flows through pipes. This lack of concordance might be explained by several factors. First, the flows experienced by colonies within pipes could have been greater than those experienced by colonies in the Rapids since the former were growing on acrylic plastic strips whose edges were oriented into the flow through the center of the pipes and which were 2 cm long in the along-stream dimension. However, calculations of turbulent boundary layer thicknesses (Vogel, 1981) for the two studies suggest that this was not the case. Turbulent boundary layer thicknesses for slow (mean flow = 0.02 m s^{-1}) and fast (mean flow = 0.15 m s^{-1}) flows in pipes were 21 mm and 14 mm respectively, assuming a downstream distance of 10 mm from the leading edge of their plastic growth strips. Corresponding thicknesses in Lough Hyne would range from 28 mm to 21 mm for slow (mean flow = 0.22 m s^{-1} ; Fig. 4) and fast (mean flow = 0.87 m s^{-1} ; Fig. 4) flows respectively, assuming a downstream distance of 0.5 m from the leading edge of fronds to the colonies. This indicates that in all situations, boundary layer thicknesses were much greater than the heights of lophophores; colonies were thus hidden from mainstream flows in both studies. The variation in growth may therefore be related to differences in the steepness of the velocity gradients within these boundary layers.

A second, and probably equally important, difference in the two studies is that Eckman and Duggins assessed the growth of juvenile colonies that were less than 2 mm in diameter at the start of the experiments (and hence were probably at the stage of having from 2–8 zooids). Colonies in our studies were not at an early astogenetic stage but had already become established in the field. These differences are illustrated by the very different growth rates in the two studies. Mean growth rates of the small colonies in Eckman and Duggins' study ranged from about 5 to $20 \text{ mm}^2 \text{ d}^{-1}$ (see fig. 4 in Eckman and Duggins, 1993) while the equivalent

mean growth rates of the larger colonies in our study were $86 \text{ mm}^2 \text{ d}^{-1}$ (SD = $55 \text{ mm}^2 \text{ d}^{-1}$) in Site 1 and $103 \text{ mm}^2 \text{ d}^{-1}$ (SD = $45 \text{ mm}^2 \text{ d}^{-1}$) in Site 2. It may be that early stages of colony development are more sensitive to flow conditions in microhabitats because arrays of lophophores and excurrent jets are not yet developed. Eckman and Duggins (1993) obtained large differences in growth rates in replicates for each of the two slower flow speeds studied (fig. 4, Eckman and Duggins, 1993). If the higher values obtained for each of these replicates are regarded as outliers due to anomalous conditions in these pipes, there is much less suggestion of a flow effect on growth across the range of the five flow speeds studied. Nevertheless, since at some point drag forces must begin to inhibit feeding, flow will eventually limit growth as Eckman and Duggins' evidence indicates. We feel the most likely explanation for our contrasting results is that colonies differed in developmental stages and experienced different velocity gradients within boundary layer microhabitats.

Other consequences of ambient flow regimes

As discussed above, miniaturization appears to be an effective means of achieving similar growth rates when colonies happen to become established in sites exposed to rapid flows. However, another consequence of living in such sites is that colonies occur at reduced densities. Thus they will experience a reduction in intraspecific competition for space, allowing individual colonies to attain larger size; it was certainly notable that, at high percent cover, colonies tended to be smaller, although we did not collect data to document this.

A possible detrimental effect of low cover is a reduction in the likelihood of achieving fertilization. *M. membranacea* releases sperm packets into the water column, where they become entrained by feeding currents. Once within the lophophore region they gain access to maternal zooids through specialized intertentacular organs of the lophophore, and subsequently effect internal fertilization of eggs within maternal zooids (Temkin, 1994). Although proximity to neighboring colonies may increase fertilization success, it is also possible that release of sperm packets into the rapid and turbulent flows in the Rapids swamps this effect, particularly since sites of high and low density are within meters of each other. We have no data on the reproductive output of colonies growing in the different ambient flow conditions to resolve this issue. Although miniaturization allows similar growth rates, it could conceivably inhibit or promote reproduction if more or less energy were allocated to growth. Also unknown is the extent to which these effects may be offset or otherwise influenced by the possibility of reaching larger colony sizes due to decreased intraspecific competition for space.

Colony hydraulics

Venting of excurrent flows as jets through chimney regions allows *M. membranacea* to avoid or at least reduce re-filtering of particle-depleted water. Chimneys in *M. membranacea* represent small regions in which zooids degenerate and are not replaced. Thus the potential contribution to feeding made by these zooids is sacrificed, presumably because the energetic gain conferred by minimizing re-filtration exceeds the cost of zooid degeneration (Lidgard, 1981). One mechanism postulated to explain the formation of chimneys is that chimneys develop when the pressure beneath the extended array of lophophores becomes greater than the array can withstand (Dick, 1987). The decrease in interchimney distances that accompanies the miniaturization of zooids in *M. membranacea* is consistent with this explanation. Smaller and shorter lophophores provide less space for excurrent water below the lophophore array. Thus, pressure develops more quickly and excurrents must be vented sooner. The notably regular spacing of chimneys in *M. membranacea* is also consistent with a hypothesis of pressure build-up under the lophophore sheet (Dick, 1987).

This postulated mechanism of pressure build-up provides a simple explanation for how *M. membranacea* can maintain functional colony-wide hydraulics across a range of ambient flow conditions, as suggested by the evidence presented here. The explanation that chimneys arise at particular developmental stages in colonies (*i.e.*, are astogenetically determined) is less satisfactory. If chimneys are astogenetically determined, interchimney distances might be expected not to vary when growth is equivalent. However, while growth for colonies at Sites 1 and 2 was not significantly different, chimneys were produced much more frequently in Site 2.

Implications of study

We have found that bryozoans show flow-dependent morphologies that result in a miniaturization of colonies with exposure to rapid flows. These morphological changes likely promote exposure to similar flow microhabitats, thereby allowing the maintenance of similar rates of feeding, and hence growth, at least up to a point. For several reasons, we suggest that these morphological changes are the result of phenotypic plasticity rather than selection for colonies with particular morphologies. Firstly, tidal flushing through the Rapids ensures that algal fronds will be subject to recruitment by the same larval pool. Secondly, there is evidence that flow regime limits active choice in habitat selection by larvae (Butman, 1987), and as all sites were subject to considerable flow, it is unlikely that larvae could discriminate amongst them. Thirdly, post-recruitment interactions are also unlikely to have selected for certain types. Colonies were chosen to be free from overgrowth interactions, and there was no evidence of predation.

The only obvious factor that could result in post-settlement mortality was flow regime itself: increased flow could have selected for miniaturized colonies. Unfortunately, we did not conduct transplant experiments; thus selection cannot be distinguished from phenotypic plasticity. However, in general, algal fronds should offer great variation in exposure to flow for encrusting bryozoans: as fronds grow, the colonies are placed in different positions both along the length of the frond and in the water column. This is particularly true since larvae of *M. membranacea* preferentially recruit to the younger regions of laminarian fronds, near the holdfasts of the plants (Brumbaugh *et al.*, 1994). Furthermore, colonies may be buffered from flows when they are growing on dense fronds within macroalgal stands but may be more exposed to flows when growing on fronds along the edges of stands. These arguments suggest that genetic specialization to narrow ranges of flow regimes is an unlikely strategy to have evolved. Rather, colonies should be able to tolerate a wide range of flow conditions since it cannot be predicted what conditions will be encountered during their lifetime. This tolerance can be achieved by phenotypic plasticity.

In the Introduction, we cited some of the many studies of feeding from flow for a variety of suspension feeders; these have provided important insights about feeding opportunities (*e.g.*, increased turbulent mixing) and constraints (*e.g.*, increased drag forces) presented by increased flow. However, a common practice in these studies has been to assess feeding across a range of flows by suspension feeders collected from particular sites (but see Okamura, 1992, and Anthony, 1997). Hence flow-dependent feeding rates of suspension feeders which themselves inhabit a range of flow environments have received little investigation, and therefore the extent to which suspension feeders may be locally adapted to flow conditions is poorly known. Thus, although studies to date reveal important information about the general effects of flow on feeding for a given situation, their results may not depict what happens in the real world since they do not take into account the longer term responses to flow by the animals in the field. However, even if many suspension feeders show plasticity in growth in response to flow, flow and feeding studies of suspension feeders collected from relatively restricted ranges of flow environments are nonetheless informative. Such studies should provide predictions about what kinds of morphological change might be adaptive under different flow conditions and may lead to insights about the significance and consequences of observed morphological variation.

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